



Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at <http://about.jstor.org/participate-jstor/individuals/early-journal-content>.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.

THE AMERICAN NATURALIST

VOL. XLV

May, 1911

No. 533

THE INHERITANCE OF POLYMORPHISM AND SEX IN *COLIAS PHILODICE*¹

PROFESSOR JOHN H. GEROULD

DARTMOUTH COLLEGE

THERE is perhaps no phenomenon of greater general interest to students of organic evolution than polymorphism, yet, although it is of frequent occurrence in insects, in few cases has it been investigated with long-continued and thorough experiments in breeding. Entomologists have usually been content to prove that different forms arise from the eggs of a single female, or of similar females of the same species, without reference to the male parent or to the immediate ancestors of the female. The time has come when these interesting phenomena, lying at the very doors of those at least who live in the country, demand more serious attention than they have yet received.

Colias philodice, the common yellow butterfly of the clover, called sometimes the clouded sulphur or roadside butterfly, is distinctly dimorphic in the female sex, in that the ground color of the wings is either yellow or white, the yellow female in most localities being much the more abundant. As this common species can readily be bred in large numbers, it affords excellent material for studying the inheritance of dimorphism limited to one sex.

¹Read before the American Society of Naturalists, December 30, 1910.

Moreover the color pattern, which is the same in both the typical yellow and the albinic variety of the female, differs in the two sexes to such an extent that they may be distinguished even in flight. The wings of the

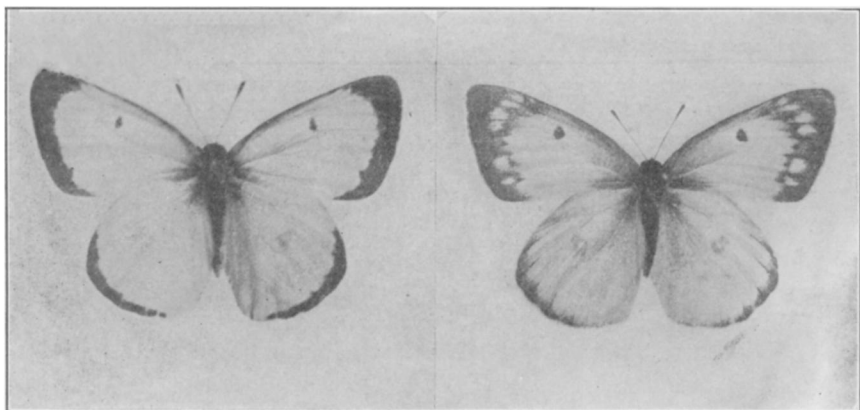


FIG. 1. *Colias philodice*. Male.

FIG. 2. Yellow female.

male (Fig. 1) are marked with a solid black band of nearly uniform width extending along their outer margins, whereas in the female (Fig. 2) the marginal band is wider on the fore wings and usually invaded by spots

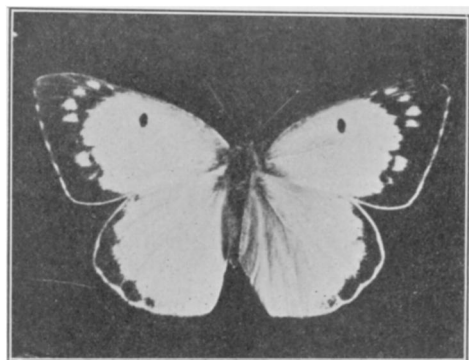


FIG. 3. White female.

of the ground color, but narrower on the hind wings and dusted with scales of yellow or, in the albinic variety, of white. The marginal band on the hind wings of the female in some individuals is absent altogether, the width of the bands in general in both sexes being very variable.

Besides these pronounced secondary sexual differences

in color and the common occurrence of the albinic female, a few specimens have been taken of an extremely rare mutation, the melanic male, in which the yellow is replaced by smoky black, the margin being distinctly paler than the ground color. In geographical distribution this aberration does not seem to follow the general rule laid down by Scudder that melanic forms occur in the southern part of the range of a species, for two of the specimens were from near Montreal, three seen and one captured at Palmyra, N. Y., and one now in the collection of Mr. H. P. Richardson, of Concord, Mass., was taken at Plainfield, Mass.

Partial melanism, or a melanistic tendency, often occurs in the female, though complete melanism has been found so far only in the male. This tendency reappears in successive generations independently of the environment, in certain strains that I have bred, though I think it possible that the action of the surroundings on certain individuals in a plastic condition may turn the germ cells in this direction. I have not yet had an opportunity to test this supposition, and my observations have been almost entirely directed to the inheritance of the albinic variety of the female.

Albinism in the genus *Colias* is due to the replacement of yellow pigment with another which is white (Fig. 3), all other pigments (black, red, etc.) remaining the same. The white is sometimes tinged with yellow, but there is a sharp difference between the color of a typical yellow female and that of the albinic form.

Albinism is not entirely confined to the females, though among the 900 descendants of white females that I have raised there has been not one white male. White males may be expected in regions where the white female is especially abundant. At Hanover, N. H., the proportion of white females to yellow is, perhaps, roughly five per cent. At Ithaca, N. Y., Professor Macgillivray informs me, the proportion of white females is considerably larger, being perhaps 10 or 15 per cent., and at Milton, Mass., Mr. W. L. W. Field estimates them at 20–25 per cent. In two localities where the white male has been

taken, about 50 per cent. of the females are white. These regions are Lava, Sullivan Co., N. Y., reported by Mr. Geo. Franck, and Alstead, N. H., on the authority of Mr. W. L. W. Field, who has seen only one white male, however, during several seasons of field work in that region.

Scudder makes the statement that "In the north this rarely, almost never, occurs in the first brood of the season, and is found much more abundantly in the latest than in the middle brood, the numbers increasing as the season advances." If this statement is true, it has an important bearing on the inheritance of the white character,² for he means, of course, that the proportions of the white females to yellow in the spring broods is less than in the later broods. My observations at Hanover in 1909, and those of my collaborator Mr. P. W. Whiting in Cambridge, Mass., in 1910, do not bear this out, for we found the white females in both places quite as common in the spring brood as in those of summer or autumn. Edwards likewise states that in the south the white form is not infrequent in the spring brood. The probable reason for Scudder's observation is that the population of the spring brood in the long run may be relatively small, because many of the hibernating caterpillars perish. The chances of finding white females in the field in the spring after a severe winter may therefore be less than during the flight of the more abundant summer broods that have not been affected by disastrous winter weather.

One of the most interesting observations that I have made during the past two seasons was the discovery of a wild female *Colias philodice* of the spring brood closely resembling *Colias nastes* of Labrador (Fig. 4), with a greenish-yellow field overspread with brownish scales, giving a grayish effect. In the margin brown replaces black. This form of female is not common, and I have seen it nowhere described. It was captured at Hanover, N. H., on June 10, 1909, and produced a brood of 34 butterflies (Fig. 5) of which 19 are males, all of which are yellow, 10 are yellow females, 5 are white females. The yellow and white colors of these offspring are of an

² See foot-note, pp. 266, 267.

unusually clear hue, and quite unlike the color of the mother.

The progeny of this female show that, supposing her to have mated with a pure yellow male not carrying white, as was probably the case, she is a heterozygote for

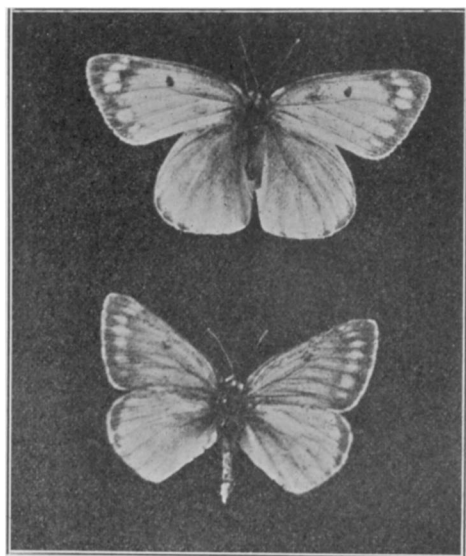


FIG. 4. The upper figure represents a spring form of female of *Colias philodice* from Hanover, N. H., resembling *C. nastes* of Labrador, shown in the lower figure.

color, potentially white, though modified probably by the effect of cold upon the chrysalis in early spring into a form strikingly like that of the Arctic species, *Colias nastes*. I hope to ascertain from caterpillars now hibernating whether this spring form may be produced at will from larvæ from a white mother by the action of cold upon the chrysalis.

My attention was attracted to the problem of inheritance of the white color in this species by certain statements in Edwards's great work on the "Butterflies of North America." He says that the progeny of an albino female are partly albino and partly yellow, or it may be all yellow. "In one instance," he says, "I had five butterflies from eggs laid by an albino, and there resulted one male and four yellow females, no albino.

In another case of four females one was an albino. Mr. Mead has met with similar results, and neither of us have known an albino to be produced from the eggs of a yellow female." These brief notes pointed

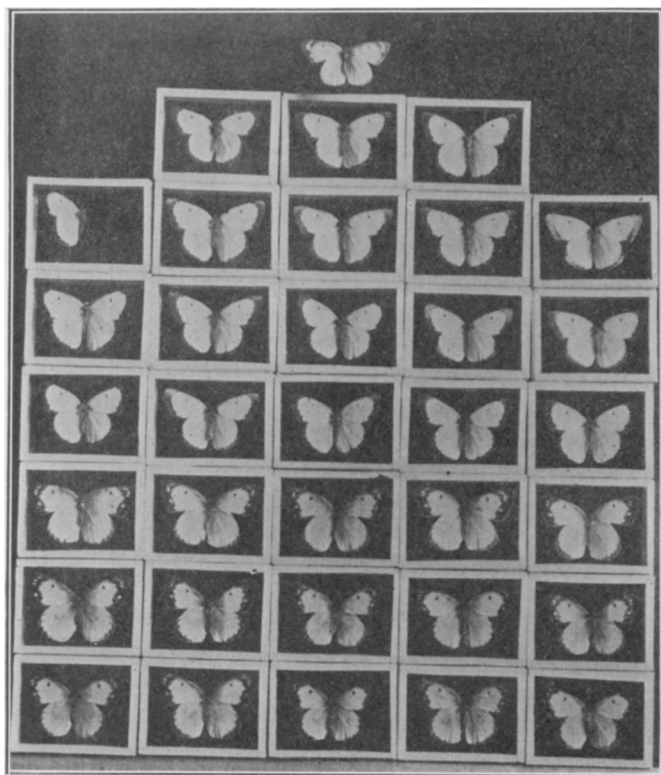


FIG. 5. The spring form of female of *Colias philodice* (at the top) and her offspring. The two rows at the bottom are yellow females; the third row from the bottom are white females. None of the offspring resemble their *nastes*-like mother.

so clearly to Mendelian inheritance that I resolved to investigate the matter, and I have thus far bred over 900 individuals from white females and from the daughters and sons of white females. In general my results differ from Edwards's observations at two points: (1) The white females always produce both white and yellow females, provided the family is large enough to represent all the possibilities. The family mentioned by Edwards, four yellow females, no white, was too small to indicate

that the mother would produce no white offspring. (2) Yellow females under certain conditions do produce both yellow and white offspring. Thus the mothers of families "e," "f," "i," and "k," 1910, were yellow, producing, respectively: 13 white and 14 yellow daughters; 7 white and 5 yellow; 30 white and 14 yellow; 19 white and 19 yellow. The conditions under which these four yellow females produced white offspring were alike. The female and the brother with which she mated were in each case the immediate offspring of a white female, the male mate in each case being presumably heterozygous for color, $y(w)$, the yellow female homozygous for that color, yy .

1. INHERITANCE OF THE WHITE FEMALE

Summary of Results

My observations, begun in the fall of 1908 and extending through the two following seasons, some of the same stock now being in hibernation, may be summarized as follows:

1. The white female, of which I have tested 13 individuals, is in all cases heterozygous for color, producing when crossed with a pure yellow male (wild, or her own brother), either equal numbers of white and of yellow female offspring, in accordance with Mendelian expectation (stock from Cambridge, Mass., families a, b, c, d, 1910), or twice as many yellow females as white (stock from Hanover, N. H., families a and c, 1909). The male offspring of a heterozygous white female are all yellow, though presumably one half are heterozygous, $y(w)$, and one half homozygous dominants, yy .

2. It is evident from these observations that white is dominant in the female, yellow in the male, these being the colors of the respective heterozygotes. This case is comparable to the results obtained by Wood in crossing horned Dorset with hornless Suffolk sheep, the male heterozygote of F_1 having horns, the ewes being hornless. The horned condition is therefore dominant in the male, while in the female hornlessness is dominant.

TABLE I

WHITE ♀⁴ [HETEROZYGOUS, w(y)] × YELLOW ♂ [HOMOZYGOUS, yy]

Mother	Father	Name of Brood	Number of Males	White Females	Yellow Females
Wild, white	Wild, yellow	1808	3	2	3
" "	" "	1909 a	39	7	16
Nastes-like form ⁵	" "	" b	19	5	10
Wild, white	" "	" c	13	3	7
Total in 1908 and 1909			74 ♂♂	17 ♀♀	36 ♀♀
Mother	Father	Brood	Males	White Females	Yellow Females
Wild, white A	Wild, yellow	1910 a	18	6	9
" " B	" "	" b	79	22	28
" " C	" "	" c	24	8	8
" " D	" "	" d	30	15	13
Total in 1910			151 ♂♂	51 ♀♀	58 ♀♀

3. If a heterozygous white female is crossed with certain other yellow males, her brothers and the sons of the same white female, that are heterozygous for color (as indicated by the fact that when mated with homozygous yellow females both white and yellow offspring result), a larger number of white females than of yellow are produced, though not three white to one yellow according to Mendelian expectation. The proportion observed is approximately two to one (viz., 38:22, 13:8, g and h, 1910, and probably the 8:4 of family 2w, 1909). This proportion may be explained, as Dr. Castle first suggested to me, by assuming that in these families no homozygous whites occur, through infertility or abortion of the "white" germ cells that would naturally combine with white, so that the offspring consist of:

♂♂ 25 per cent. homozygous yellow, yy, and 50 per cent. heterozygous yellow, y(w).

♀♀ 25 per cent. homozygous yellow, yy, and 50 per cent. heterozygous white, w(y), no pure homozygous whites of either sex occurring in my cultures.

⁴ The sign ♀ stands in Tables I-VI for the white female, ♀ for the yellow female.

⁵ This individual is possibly a pure yellow (yy) ♀, modified by cold and mated with a heterozygous y(w) male. It is possible that this brood should be included in Table IV.

TABLE II

WHITE ♀ [HETEROZYGOUS, W(Y)] × YELLOW ♂ [HETEROZYGOUS, Y(W)]

Mother (white)	Father (yellow)	Brood	Males	White Females	Yellow Females
1d ³⁶	* 1d ⁸ ♂	l	4	3	3
1d ³⁹	† 1d ¹⁸	g	63	38	22
1d ⁴⁵	“	h	16	13	8
Total			83 ♂ ♂	54 ♀ ♀	33 ♀ ♀

TABLE III

WHITE ♀ [HETEROZYGOUS, W(Y)] × YELLOW ♂ [UNTESTED, YY OR Y(W)]

Mother (white)	Father (yellow)	Brood	Males (yellow)	Females (white)	Females (yellow)
a ³⁵ ♀	a ⁶ ♂	1909, 2w	20	8	4
4b ²¹	4b ¹⁵	1910, m	9	5	3
1b ³⁹	1b ³¹	o	9	3	4
Total			38 ♂ ♂	16 ♀ ♀	4 ♀ ♀

Thus here is a case comparable to that of yellow mice, which, as shown by Cuénot, Castle and others, are always heterozygous, homozygous yellow mice not being produced; so that the proportions obtained by mating yellow mice together is 66.6 per cent. yellow, 33.3 per cent. non-yellow.

4. The wild white males which occur rarely are presumably recessive homozygous whites, but none have yet appeared in my crosses of heterozygous yellow males with heterozygous white females (g and h, 1910), and I have not yet had an opportunity to test their possibilities in breeding.

TABLE IV

YELLOW ♀ [HOMOZYGOUS, YY] × YELLOW ♂ [HETEROZYGOUS, Y(W)]

Mother (yellow)	Father	Brood	Males	White Females	Yellow Females
a ¹⁴ ♀	a ⁷ ♂	1910, e f k i	58	13	14
a ¹⁰	a ¹⁹		10	7	5
1d ³⁰	‡1d ⁸		46	19	19
1d ⁴⁶	‡1d ¹⁸		27	30	14
Total			141 ♂ ♂	69 ♀ ♀	52 ♀ ♀

* Tested by crossing with 1d³⁰ ♀ (yellow). See Table IV.

† Tested by crossing with 1d⁴⁶ ♀ (yellow). See Table IV.

‡ See Table II.

TABLE V

YELLOW ♀ [HOMOZYGOUS, YY] × YELLOW ♂ [HOMOZYGOUS, YY]

Mother (yellow)	Father	Brood	Males	White Females	Yellow Females
a ²⁴	a ⁶ , a ²³ , a ²⁶ or a ⁴²	1909, 2y	20	0	15

Total number of males 507

Total number of females 412

TABLE VI

THE RESULTS OF BREEDING EIGHT DIFFERENT PURE LINES OF STOCK
DURING 1908-1910. Brackets enclose designations of individuals
used in subsequent breeding

Mother	Father	Brood	♂ ♂	White Females ♀ ♀	Yellow Females ♀ ♀
1908 Wild, white	Wild, yellow	3	2	3
1909 A ♀ a ³⁵ ♀ a ²⁴ ♀	“ “ a ⁶ ♂ Either a ⁶ , a ²³ , a ²⁶ or a ⁴²	1909 a 2w 2y	39[a ⁶ ♂, <i>et al.</i>] 20 20	7 [a ³⁵ ♀] 8 0	16 [a ²⁴ ♀] 4 15
1909 B <i>Nastes</i> -like form	Wild, yellow	b	19	5	10
1909 C Wild, white	“ “	c	13	3	7
1910 A Wild, white	“ “	1910 a	18 [a ⁷ a ¹⁹]	6	9 [a ¹⁴ ♀ a ¹⁰ ♀]
a ¹⁴ ♀ a ¹⁰ ♀	a ⁷ ♂ a ¹⁹ ♂	e f	58 10	13 7	14 5
1910 B Wild, white	Wild, yellow	b	79 [4b ¹⁵ ♂ 1b ³¹ ♂]	22 [4b ²¹ ♀ 1b ³⁹ ♀]	28
4b ²¹ ♀ 1b ³⁹ ♀	4b ¹⁵ ♂ 1b ³¹ ♂	m o	9 9	5 3	3 4
1910 C Wild, white	Wild, yellow	c	24	8	8
1910 D Wild, white	“ “	d	30 [1d ⁸ 1d ¹⁸]	15 [1d ³⁶ 1d ³⁹ 1d ⁴⁵]	13 [1d ³⁰ 1d ⁴⁶]
1d ³⁹ ♀ 1d ⁴⁵ ♀ 1d ⁴⁶ ♀ 1d ³⁰ ♀ 1d ³⁶ ♀	1d ⁸ ♂ “ “ 1d ⁸ ♂ “	g h i k l	63 16 27 46 4	38 13 30 19 3	22 8 14 19 3

If the proportion of yellow females to white is really greater in the spring brood than in those of summer and especially autumn, as Scudder states, then it would be evident that some of the yellow females of the spring brood are heterozygous for color. See p. 260.

5. Yellow daughters of a white female are probably all homozygous for yellow.³ When crossed with certain of their brothers, presumably heterozygous for color, these yellow females produce both yellow and white female offspring, sometimes in equal numbers, in accordance with Mendelian expectation (broods e, f, k), but sometimes twice as many white as yellow (brood i).

6. Yellow homozygous females, daughters of a white female, when mated with other brothers presumably homozygous produce only yellow offspring (brood 2y, 1909).

2. INHERITANCE IN *Colias Edusa*

The numbers of typical orange and of white females of the European *Colias edusa* obtained by Frohawk (1901) from the eggs of four wild white females (var. *helice*), viz., 110 white ♀♀ (*helice*) and 125 orange ♀♀ (*edusa*) with 302 ♂♂, are in approximation to equality, and point to the conclusion that, in this species also, the white female is heterozygous for color.

Harrison and Main (1905) raised from the eggs of a white female (*helice*) of this species 79 ♂♂, 52 ♀♀ *helice* (white), and 19 ♀♀ *edusa* (orange). The numbers indicate that in this case both the parents were probably heterozygous for color. All the male offspring were of the typical orange hue, so it may be assumed that the 25 per cent. of homozygous white males that would be expected from mating two heterozygotes together were aborted, though the numbers indicate that 25 per cent. of the females were homozygous in whiteness. The expectation in the distribution of the observed number (71) of females would be

³ It is of course not impossible that yellow females that are heterozygous for color may exist, and that this may account for the excess of yellow females over white in broods a, b and c, 1909. In order to test this matter and to determine whether, when a pair of yellows throw white, it is the male or the female that carries the white, the male crossed with any yellow should first be mated with a female known to be of a pure yellow strain. If such a pair throws only yellow, he is of course pure yellow, and if he is then paired with a yellow, and white offspring should appear, the occurrence of a yellow heterozygous female would be demonstrated, but if he has produced white offspring with a pure yellow female, he is assuredly a heterozygote, and will have some white daughters when paired with any yellow female.

$17\frac{3}{4}$ homozygous white, ww, + $35\frac{1}{2}$ heterozygous white, w(o), + $17\frac{3}{4}$ homozygous orange, oo, = $53\frac{1}{4}$ white [ww + w(o)] + $17\frac{3}{4}$ orange, which accords closely with the actual count, viz., 52 white (*helice*), 19 orange (*edusa*).

3. GENERAL OBSERVATIONS ON THE GENUS *Colias*

Since the female color pattern is the one that prevails in both sexes when there is no differentiation (*e. g.*, *Colias nastes*, *C. hyale*, etc.) I am inclined to the view that in this genus of butterflies at least, as probably in birds, the secondary sexual characters of the male represent a more highly modified, those of the female a more primitive, condition. We may recognize in this country, as in the eastern continent, a natural series of species of the genus *Colias*, at the beginning of which stands the undifferentiated Arctic *Colias nastes* of Labrador, Greenland, northern British America and Alaska, with the female color pattern, and a dull greenish yellow ground color suffused with brown, common to both sexes. This ground color, as my brood of *Colias philodice*, 1909, b, shows, is closely related to white and probably interchangeable with it. Next in the series are the subarctic *C. pelidne* and *C. scudderi*, in the males of which the yellow color and black color pattern typical of many species of *Colias* attain their full development, while all the females are clear white, with faint marginal dark bands.

The yellow ground color and the solid black marginal band probably arose by mutation in an undifferentiated *nastes*-like or white stock, and at once became dominant in the male, while the original colors and color pattern remained dominant in the female.

Southward from the range of *C. pelidne*, in the Canadian faunal region, is the closely related *C. interior*, in which yellow females (var. *laurentina*) occur, though white females are "on the whole commoner" according to Scudder, and from this region southward extends *C. philodice*, in which the yellow females generally are far more abundant than the white. Finally, the orange color of *C. eurytheme* of the central and western states, in

which species a most complicated polymorphism occurs, probably represents a stage in evolution beyond the yellow, as does also the black of the melanic male mutant of *Colias philodice*.

The view that the color and color pattern of the male butterfly diverge more widely from the typical coloration of the group to which the species belongs, than those of the female, though advocated by Darwin, 1871, was strenuously opposed by Scudder ('89, Vol. 1, p. 531), who cites the white female of *Colias philodice* as evidence to support his position. The case of *Argynnis diana*, in which the dark blue female differs much more widely from the usual tawny color of the fritillaries than does the male, certainly points strongly to Scudder's view, but it may well be that no one rule applies to all genera of butterflies, though there are in butterflies and in birds few if any exceptions to the law that the plumage of the male is more brilliantly colored and more highly differentiated than that of the female.

4. INHERITANCE IN *Papilio memnon*

Jacobson's observations on the Javan butterfly *Papilio memnon*, in which there are three varieties of female, and the discussion of them by de Meijere, 1910, show that, as in *Colias*, the dominant form among the females is the one most unlike the male, viz., the brownish, tailed *Achates*; the form that is recessive in the female, as in *Colias* also, is the one most like the male, viz., the dark tailless *Laocoon*. The intermediate variety, *Agenor*, is heterozygous, epistatic to *Laocoon* but hypostatic to *Achates*. In the male the dark color, recessive in the female, is completely dominant.

Inspection of Jacobson's results leads one to believe that two, or probably three, pairs of unit characters are involved, and that not all of the individuals recognized as *Achates* or as *Agenor* are of the same gametic constitution. The remarkable fact brought out by Jacobson is that, in the various combinations made, only two of the three varieties of female were obtained in any one brood.

As a working hypothesis, I regard the dominant female

form (the brownish tailed *Achates*) as the original type, from which the tailless dark-colored male and the somewhat similar *Laocoon* have been derived by mutation, in the same way that the white color, dominant in the female but recessive in the male of *Colias*, may be postulated as the ancestral color in that genus.

5. INHERITANCE OF SEX

Discussion of the inheritance of sex in *Colias philodice* at present must deal in part with unverified hypotheses, because I have not yet secured and tested white males nor, if they exist, homozygous white females. Since, however, all other possible combinations have been realized, these may now be reviewed, and tentative predictions made as to what progeny may be expected in the future from homozygous white stock in its various combinations.

Let us suppose that the male color pattern and all primary and secondary sexual characters of the male are dependent upon the presence of a "determiner" for which the male individual is a homozygous dominant (xx), while the female individual is heterozygous, one half of the gametes which it produces containing the determiner (x) and one half lacking it (o). Thus the gametic constitution of the female may be represented as xo, that of the male as xx.

Taking color into consideration, the nature of the pure yellow male may be represented by the symbol: yyxx, that of the pure yellow female as yyox. Furthermore, if yellow is dominant in the male, and white in the female the male heterozygote would be y(w) xx, while the white female would have the symbol w(y) ox. Such a white female, being heterozygous in both color and sex, may be further assumed to produce in equal numbers gametes of four kinds. This hypothesis will appear perhaps more firmly grounded if we imagine that both of the mitoses which give rise to the polar bodies are differential divisions, instead of one being an equational division and one a differential division, as is usually as-

sumed or demonstrated to be the case. The eggs of the white female are, accordingly, to be represented as follows: yx , yo , wx , wo ; those of the yellow female: yx and yo . It is not necessary to assume in gametogenesis of the heterozygous white female of *Colias* any repulsion between one determiner and another resulting in a coupling such as is believed to occur in *Abraaxas*. The determiner for yellow and that for white have equal chances of passing into a gamete with the male determiner or into one without it.

There are, of course, nine imaginable sets of combinations that would take place in the fertilization of the eggs of a species with three sorts of females: $yyox$, $w(y)ox$ and $wwox$ by the sperms of the males: $yyxx$, $y(w)xx$ and $wwxx$. We will consider first the combinations that up to the present time actually have been made in my cultures.

1. THE PURE YELLOW FEMALE \times THE PURE YELLOW MALE

$yyox \times yyxx$

yx , yo = gametes of the female

yx , yx = gametes of the male

$yyxx$, $yyox$ = 50 per cent. pure yellow ♂♂, 50 per cent. pure yellow ♀♀.
(Brood 2y, 1909.)

2. THE PURE YELLOW FEMALE \times HETEROZYGOUS YELLOW MALE

$yyox \times y(w)xx$

yx , yo = gametes of the female

yx , wx = gametes of the male

$yyxx$, $yyox$, $y(w)xx$, $w(y)ox$

25 per cent. pure yellow ♂♂, 25 per cent. pure yellow ♀♀, 25 per cent. heterozygous yellow ♂♂, 25 per cent. heterozygous white ♀♀, all the males being yellow, and the females yellow and white in equal numbers. (Broods e, f, k, i.)

3. WHITE HETEROZYGOUS FEMALE \times PURE YELLOW MALE

$w(y)ox \times yyxx$

wx , wo , yx , yo = gametes of the female

yx , yx = gametes of the male

$y(w)xx$, $w(y)ox$, $yyxx$, $yyox$

♂♂ 50 per cent. pure yellow, 50 per cent. heterozygous yellow,
♀♀ 50 per cent. pure yellow, 50 per cent. heterozygous white,
all the male being yellow, the females yellow and white in equal numbers. (Broods a, c, 1909; a-d, 1910.)

4. WHITE HETEROZYGOUS FEMALE \times HETEROZYGOUS YELLOW MALE

$$\overline{w(y)ox} \times y(w)xx$$

wx, wo, yx, yo = gametes of the female

yx, wx = gametes of the male

$$y(w)xx, w(y)ox, yyxx, yyox$$

$$y(w)xx \quad w(y)ox$$

wwxx wwox. Assuming that the last two combinations (homozygous whites) are cancelled, we should have:

♂♂ 25 per cent. pure yellow, 50 per cent. heterozygous yellow,

♀♀ 25 per cent. pure yellow, 50 per cent. heterozygous white.

This combination has also been accomplished in my cultures, *e. g.*, broods g and h, 1910.

The five possible remaining combinations may never be completely realized owing to partial or complete infertility of the homozygous white stock. However, white males do occur, and assuming that homozygous white zygotes might be successfully produced, the resulting combinations would be as follows:

5. PURE YELLOW FEMALE \times HOMOZYGOUS WHITE MALE

$$yyox \times wwxx$$

yx, yo = gametes of the female

wx, wx = gametes of the male

$y(w)xx, w(y)ox$, that is, both males and females would be heterozygous for color, all the males being yellow, all the females white.

6. HETEROZYGOUS WHITE FEMALE \times HOMOZYGOUS WHITE MALE

$$w(y)ox \times wwxx$$

wx, wo, yx, yo = gametes of the female

wx, wx = gametes of the male

wwxx, wwox, $y(w)xx, w(y)ox$, giving

♂♂ 50 per cent. heterozygous yellow, 50 per cent. homozygous white,

♀♀ 50 per cent. heterozygous white, 50 per cent. homozygous white,

thus all the females would be white, but the males yellow and white in equal numbers.

7. HOMOZYGOUS WHITE FEMALE \times PURE YELLOW MALE

$$wwox \times yyxx$$

wx, wo = gametes of the female

yx, yx = gametes of the male

$y(w).x, w(y)ox$, or the males all heterozygous yellow, the females all heterozygous white [the same result as in (5)].

8. HOMOZYGOUS WHITE FEMALE \times HETEROZYGOUS YELLOW MALE $wwox \times y(w)xx$ $wx, wo =$ gametes of the female $yx, wx =$ gametes of the male $y(w)xx, w(y)ox, wwxx, wwox, \text{ or}$ σ^8 50 per cent. yellow, heterozygous, 50 per cent. pure white, ϕ^8 50 per cent. white, heterozygous, 50 per cent. pure white.9. HOMOZYGOUS WHITE FEMALE \times HOMOZYGOUS WHITE MALE $wwox \times wwxx$ $wx, wo =$ gametes of the female $wx, wx =$ gametes of the male $wwxx, wwox, \text{ or the males all homozygous white, the females all homozygous white.}$

That the germ cells in the white female, which I have shown to be heterozygous for color, and which is presumably also heterozygous for the sex determiner, are really segregated in oogenesis into four distinct groups is strongly indicated by the realization of the results of this hypothesis as shown in ¶¶ 3 and 4. In this segregation there is no real "coupling," the sex determiner (x) being equally distributed among the white and the yellow gametes, but the chances are also equal that any gamete may receive the x factor, and become a male zygote when fertilized, or lack it, and become on fertilization a female organism.

As would be expected, there are similarities between *Colias* and *Abraxas*⁶ in the method of inheritance of the white female variety in each. The female in both is heterozygous for sex, producing in equal numbers eggs which give rise to males and to females when fertilized by the like sperms of the homozygous male. But there are striking differences between the two forms in inheritance, *e. g.*, the dominance of the type color in *Abraxas*, compared with its dominance in the male only in *Colias*, white being dominant in the female; females of the type form that are homozygous for color are found in *Colias*, but not in *Abraxas*, in which all the type females are heterozygous, just as are all the white females of *Colias* that have hitherto been bred. The segregation of the

⁶ Doncaster, L., 1908, Rept. Evol. Committee Roy. Soc., IV, p. 53.

color and sex determiners in the *grossulariata* female and the white female *Colias*, both of which are heterozygous in these two respects, takes place presumably by quite different methods. Other differences or similarities will doubtless come to light when the white male of *Colias* is bred.

The notation which I have here used to express the gametic constitution of *Colias* applies equally well to *Abraxas*, assuming that maleness is dominant and that in gametogenesis of the heterozygote for color and sex, viz., the female *grossulariata*, GLOX, the male determiner, X, accompanies into one gamete the determiner for high color, G; while the determiner for the undeveloped color, L, is coupled with that for the undeveloped (female) sex, viz., O. This seems to me to be a more plausible way of expressing the combinations demanded by the results than that there is a "repulsion" between the determiner for femaleness (which is assumed in this view of the case to be dominant) and that for the dominant strong color, G, as suggested by Bateson and Punnett.

On the other hand, it is true that their assumption that in *Abraxas* the male is a homozygous recessive may be applied equally well to *Colias*. However, I am constrained to adopt the view that the male in both is a homozygous dominant for the following reason:

Dominance in the male postulates the presence in all the sperms and in half the eggs of a chemical substance which in double quantity in an oosperm so stimulates it that the male characters, both primary and secondary, one by one make their appearance; while in single quantity (introduced by the sperm only) a lesser stimulus is given, and the organism develops in lesser degree along different lines into the female form. This hypothesis carries within itself an "explanation," feeble though it be, of the male form and color pattern, as well as of those of the female. It is in harmony with the fact that the intenser color of the male butterfly or moth, generally, represents a more advanced condition in the evolution of pigment than the paler colors of the female.

If, on the other hand, following the interpretation of

Doncaster's results given by Bateson and Punnett, 1908, and by Castle, 1909, viz., that the male is recessive and the sperms contain no sex determiner, which is presumed to be present in half of the eggs only, then we must imagine that a single quantity of this determiner raises one oosperm to the female condition, while, in the entire absence of it, it is understood that another oosperm proceeds to the development of the frequently more complex organs and generally brighter colors of the male.

In using a modification of the convenient notation for sex-limited characters devised by Wilson and modified by Castle to express the parallelism between recent discoveries in cytology and Mendelian segregation, I do not wish to imply that the symbol X, as applied to *Colias*, refers to any sort of chromosome. Nor is there, so far as I know, any cytological evidence as to the dominance or recessiveness of the homozygous male condition in the possibly large class of cases like *Abraxas* and *Colias* in which the female is presumably heterozygous for the sex determiner.

As Castle, 1909, has shown, there are two categories of cases in sex inheritance: viz., (A) those in which the female is assumed to be a homozygous dominant for the sex-determining factor (XX), while the male is a heterozygote, producing two sorts of spermatozoa that are not only physiologically but presumably even morphologically different. This category is illustrated cytologically by the extreme case of *Anasa*, in which one set of sperms, the male-producing, contain only four chromosomes each, while the other, the female-producing, have five, the number characteristic of all the eggs. The second class of cases (B) is that including *Abraxas* and *Colias*, in which the peculiarities of their inheritance can be explained by assuming that the female is heterozygous for the differential sex factor, producing two types of eggs, one destined, when fertilized by the sperm of the homozygous male to produce only males, the other only females. Furthermore Castle, following Bateson and Punnett, 1908, regards maleness as recessive, the oosperm contain-

ing only one sex factor, viz., that brought in by the spermatozoon.

The field represented by class A has naturally been well explored by cytologists, for in spermatogenesis the odd chromosome was discovered, and there it is expected; moreover the study of spermatogenesis is attended with less difficulty than oogenesis. Hence comparatively few observers have paid any attention to the behavior of the chromosomes in the maturation of the egg, and cytological evidence of the occurrence of possibly dimorphic eggs in the second class of cases is lacking, though Balzer's 1908 observations on oogenesis in the sea-urchin, mentioned by Wilson, 1909 b, indicate that something may be done along this line.

The cytological evidence bearing upon the Lepidoptera, so far as it goes, however, indicates that the male is morphologically homozygous. There is no dimorphism of spermatozoa, the same number of chromosomes being found in all the spermatids. There is, however, a heterochromosome, interpreted by the various observers as a pair of equal idiochromosomes, associated with the plasmosome in the growth period. According to Dederer, 1907, and Cook, 1910, it ultimately becomes indistinguishable from the other chromosomes, though in the butterfly and the moth examined by Stevens, 1906, its large size made it visible through the maturation mitoses, in both of which it divides into equal parts. Thus, in the seven moths and one butterfly (*Euvanessa antiopa*) examined by these observers, there is cytological evidence, if the chromosome theory of sex determination be assumed, that the male is homozygous. Unfortunately we have no exact information, so far as I am aware, as to oogenesis in butterflies. If it should be shown that in Lepidoptera there is a visible dimorphism of ova as regards the number of chromosomes, the cytological interpretation of sex determination would receive an interesting and important confirmation.

If such visible dimorphism should be discovered, it would be most interesting to see what bearing it has, if any, upon the question whether the homozygous male is

dominant or recessive. If the latter be indicated, then we may find that a suitable designation of the gametes of *Abraxas* and *Colias* would be that suggested by Wilson, 1909 b, viz., for the male YY and for the female XY, Y being the small synaptic mate of X, which is the large odd "female-producing" chromosome.

On the other hand, if the male is dominant a state of affairs that is exactly the reverse might be expected, viz., an absence of a chromosome, or an abnormally small one, in half of the eggs would be the visible sign of future femaleness. If these conditions should be realized, we might be able to identify the "equal idiochromosomes" already found in the spermatogenesis of butterflies with my XX of the male, the corresponding chromosome in the male-producing type of egg being X, the female-producing ova either lacking the chromosome altogether or having one of reduced size.

Dr. Castle, in a recent letter to me, expressed the opinion that the well-known anabolic tendency of the female, especially in reproductive activities, renders it extremely probable, on the other hand, that the female-producing gamete in every case of disparity should have the larger chromatic equipment. This seems to me very plausible, and it may well be that the findings of cytology in reference to this question can never do more than demonstrate the presence of this constant anabolic tendency in the female-producing gametes. The appearance of the large X chromosome in the female-producing gamete of the Hemiptera may be, therefore, only the visible expression of a sex tendency already established, as Morgan's observations on the cytology of *Phylloxera* indicate.

But the demonstration of this anabolic tendency, even in the unfertilized gamete, does not mean necessarily the *presence* of a sex determiner that is absent or deficient in the male-producing gamete, and hence the *dominance* of femaleness. It is just as reasonable to assume that the constant katabolic tendency of the male, evinced possibly by deficiency in chromatin at the start and certainly by the presence of horns, high colors and elaborate plumage

in adult life in many animals, is due to the excess of some hormone in a gamete which thereby becomes male-producing, in other words, to a *dominance of maleness*. On the other hand, in the absence of such an excitant, the recessive condition of femaleness would result, with a constant tendency towards quiescence, towards the accumulation of reserves of food to nourish the offspring, and the absence in the adult of the brilliant colors, horns and all the well-known and highly specialized secondary sexual characters of the male.

If it should be proved that maleness is dominant in lepidoptera in which the female is sexually heterozygous, may it not be true, on the other hand, that femaleness is dominant in the forms in which the male is heterozygous for sex, as in Castle's class A?

I see no inconsistency in these two antithetic categories, but should expect to find in the latter either that the female, and not the male, is the more variable, active and progressive, as in the bee, or that, as in hemiptera, both sexes are in external appearance and in habits much alike.

In brief, I have tried to point out in this discussion that a different interpretation from that of Castle may be applied to the case of *Abraxas*, and of *Colias* also, viz., that these cases, and others that may fall into the same category, differ from those of the well-established class A of Castle in that one is the exact reverse of the other, the female in class A being a homozygous dominant for the sex determiner, whereas in class B the male is a homozygous dominant, and not a homozygous recessive as has hitherto been assumed. The view here set forth not only accounts for the facts of Mendelian inheritance in these two insects equally as well as the other, but has the added advantage of harmonizing with the facts regarding the secondary sexual characters in lepidoptera and birds.⁷ The high colors and elaborate plumage of the

⁷ The recent experiments of Goodale, however, described in the *Biological Bulletin*, Vol. 20, No. 1, December, 1910, show that the removal of the ovaries from the Rouen duck produces a gradual tendency toward the assumption of the male plumage which is not in accordance with the view that

male are dominant characters eventually produced in the adult, according to my view, by the presence in the oosperm of a double quantity of a male-producing enzyme or similar substance. This hypothesis does not depend upon cytology for its support, though it is not impossible that future discoveries in oogenesis may be found to be in harmony with it.

6. DIMORPHS

If complete separation of the yellow- and the white-bearing gametes should fail to occur in the oogenesis of the white female of *Colias*, in the differential division of an oocyte destined after fertilization to become a female individual, then the right wings of the future butterfly might be white, the left yellow, or *vice versa*. Such an individual, captured by Mr. J. H. Rogers, Jr., of Medford, Mass., is figured in *Psyche*, Vol. X, Pl. X, Fig. 4. A similar specimen of *Colias edusa*, the right wings being white, is figured by Fitch, 1878, in the *Entomologist* (No. 178, pp. 49-61). Fitch shows also a female with the fore wings white and the hind wings yellow. A gynandromorph might be produced by similar failure in the separation of a gamete containing the sex determiner from one lacking it. Various combinations of color and sex are theoretically possible in one individual, if we assume that imperfect division of the gametes may occur in gametogenesis. The discovery of these combinations in nature, or their production by artificial disturbance of the ova, is well within the limits of possibility.

The production of a dimorph with one side yellow and one white is easily explained if we assume, for example, that the determiners for yellowness and for whiteness, after synapsis, reside in a single bivalent chromosome, which fails to divide differentially in oogenesis, but passes over bodily into one of the gametes, the egg. If

the male in birds owes his more brilliant plumage to the addition of something to the female type.

the first cleavage completes the differential division of the bivalent chromosome, instead of dividing it lengthwise, the right and left dimorphism is easily understood. Or we might postulate the suppression altogether of the differential oogenetic division of the egg of a white heterozygous, $w(y)$, female of *C. philodice* which normally results in the separation of color potentials, but it is questionable whether under such conditions the egg would develop.

Again, the theory of Boveri, 1902, that a gynandromorph is produced if a spermatozoon (sperm nucleus) unites with one of the two nuclei in the two-cell stage, instead of with the original egg nucleus; or that of Morgan, 1907, that two sperms enter, one uniting with the egg nucleus and (in the bee) determining the female half, while the other gives rise to the male half, may be applied to these dimorphs. According to Boveri's view, for example, we have to assume in the case of *Colias* that a "white" sperm from a heterozygous yellow male enters a "yellow" egg containing no sex determiner, and after awaiting the precocious division of the egg nucleus, unites with one of the two nuclei thus produced, and determines the character of the white, or hybrid, half of the resulting female organism.

7. PRECOCITY OF THE MALES

Males of *Colias philodice*, as in certain other lepidoptera, not only appear in the fields earlier than the females in the spring, summer, and autumn broods, but also, in every family of this species that I have raised, a very large proportion of males emerge from the chrysalis early in the period during which eclosion takes place. Thus, as shown by Table VII, in brood a, 1909, 28 males emerged from the chrysalis at the beginning of the period of eclosion, while only 3 females emerged during the same time, and, of the first half of the brood to pupate, 26 proved to be males and only 5 females. In general, 82 per cent. of the first half of the four broods for which data are here presented to reach the pupal

stage were males, only 18 per cent. females. The remaining individuals of these four families, constituting the second half of each in reaching the pupal stage, were, on the other hand, largely females (66 per cent.), only 34 per cent. being males.

These facts led me to entertain the idea that the eggs which are to become males may be laid before the female-producing ova. To test this hypothesis, I segregated the successive batches of eggs laid by seven females in 1910, and reared the larvæ of each successive batch separately, to see if the lots laid first by each female would contain a larger proportion of males than those laid later. It will be seen from Table VII that in families b, c, d and e there was in each case a slightly larger proportion of male eggs in the first laying than in the batches laid subsequently, but in families g, i and k exactly the reverse is true, the last lots of eggs laid by each female (viz., 3g and 4g, 2i, and 3k and 4k) containing more males than females. It is evident, therefore, that the male-producing ova are not laid on the average earlier than those that are female-producing, but that the larval period of the male is shorter than that of the female.

In consequence of this fact it is not surprising to find that when a brood of caterpillars is exposed to any adverse conditions such as starvation, an excess of male butterflies, as Mrs. Treat long ago found, will result, for the simple reason that many females, exposed to adverse conditions during a longer period of growth than that of the males, have been eliminated, while the more precocious male caterpillars survive in greater numbers. This will explain, I believe, the excess of males in my cultures, 507, or 55 per cent. of the total number being males, 412, or 45 per cent. being females. There is no evidence, however, of any differential death rate between the yellow and the white females. Neither is more precocious in larval development than the other, and intestinal diseases appear to strike each with equal virulence.

TABLE VII

PRECOCITY OF MALES IN *Colias philodice*

Year	Brood	First Half of Brood to Pupate		Dates of Pupation	Second Half to Pupate		Dates of Pupation	First Ecllosion
		♂ ♂	♀ ♀		♂ ♂	♀ ♀		
1909	a	26	5	June 25-29	13	18	June 29- July 1	July 2-9 ♂ ♂ ♀ ♀ 28 3
1909	b	14	3	July 2-4	5	12	July 4-6	
1909	c	10	1	July 7-10	3	9	July 11-13	
1910	a	13	4	July 9-13	5	11	July 13-19	
Total		63 ♂ ♂	13 ♀ ♀		26 ♂ ♂	50 ♀ ♀		

Eighty-two per cent. of first half of all broods in reaching the pupal stage are males.

Thirty-four per cent. of the second half of broods in reaching the pupal stage are males.

Year	Brood	Males	Fe- males	Per Cent. of Males	Brood	Males	Fe- males	Per Cent. of Males
1910	1b	33	12	73 from 1st batch	1g	16	13	55
	2b	7	3	70 from 2d batch	2g	18	23	44
	3b	9	7	56 from 3d batch	3g	21	19	52.5
	4b	30	28	51.7 from 4th batch	4g	8	5	61.5
	1c	20	13	60.6	1i	13	22	37
	2c	4	3	57	2i	14	22	38.8
	1d	12	10	54.5	1k	8	11	42
	2d	7	6	53.8	2k	15	12	55
	3d	11	12	47.8	3k	13	10	56.5
					4k	10	5	66.6
	1e	13	3	81.2				
	2e	18	12	60				
	3e	27	12	69				

These investigations are by no means finished, and any one who should chance to capture any unusual specimen of this species, or of any closely allied to it, showing melanistic or other aberrant tendencies, would confer a great favor on the writer of this paper by mailing to him the specimen alive in a metal box lined with moist filter paper sewed firmly against the perforated sides. A white male is, of course, especially desired.

In conclusion, the writer wishes to express his hearty thanks to his friend Mr. P. W. Whiting, an accomplished student of butterflies, for his kind and efficient cooperation in the field work connected with these studies and in the laborious processes of preparing specimens for detailed examination. The friendly counsel of Dr. W. E. Castle has been also of great value to the writer in

entering this to him new but extremely fascinating field of investigation.

REFERENCES TO LITERATURE

- Baker, F., '08. *Verh. d. deutsch. Zool. Gesell.* [Reference from Wilson, 1909.]
- Bateson, W., and Punnett, R. C., '08. The Heredity of Sex. *Sci.*, Vol. 27, No. 698, pp. 785-787, May 15, 1908.
- Boveri, T., '02. Ueber mehrpolige Mitosen als Mittel zur Analyse des Zellkerns. *Verh. phys. med. Gesell. Würzburg*, XXXV. [Ref. from Morgan, 1907.]
- Castle, W. E., '09. A Mendelian View of Sex Heredity. *Sci.*, Vol. 29, No. 740, March 5, pp. 395-400.
- , '10. On a Modified Mendelian Ratio among Yellow Mice. *Sci.*, Vol. 32, No. 833, December 16, 1910, pp. 868-870.
- Cook, M. H., '10. Spermatogenesis in Lepidoptera. *Proc. Acad. Nat. Sci. Phila.*, April, 1910, pp. 294-327, Pl. XXII-XXVII.
- Darwin, C., '71. Descent of Man. Vol. I, Chap. 11.
- Dederer, P. H., '07. Spermatogenesis in *Philosamia cynthia*. *Biol. Bull.*, Vol. 13, No. 2, pp. 94-105.
- Doncaster, L., and Raynor, '06. *Proc. Zool. Soc. London*, Vol. I, p. 125.
- Edwards, W. H., '68-'93. The Butterflies of North America. 3 vols., Boston.
- Frohawke, F. W., '01. On the Occurrence of *Colias edusa* and *C. hyale* in 1900, and the Results of Rearing the Variety *helice* from *helice* Ova. *Entomologist*, Vol. 34.
- Jacobson, E., '10. Beobachtungen über den Polymorphismus von *Papilio memnon* L. *Tijdschrift voor Entom.*, Bd. 52, pp. 125-157.
- Main, H., and Harrison, A., '05. *Trans. Entom. Soc. London*, 1905, p. VI.
- Meijere, J. C. H. de, '10. Ueber Jacobsons Züchtungsversuche bezüglich des Polymorphismus von *Papilio memnon* L. ♀, und über die Vererbung secundärer Geschlechtsmerkmale. *Zeitsch. f. indukt. Abstamm. u. Vererbungslehre*, Bd. 3, No. 3, pp. 161-181, March, 1910.
- Morgan, T. H., '07. Experimental Zoology. Chap. 27, p. 407. New York.
- Scudder, S. H., '89. The Butterflies of the Eastern United States and Canada. 3 vols., Cambridge, Mass.
- Stevens, N. M., '06. Studies in Spermatogenesis, II. Pp. 33-58, Pl. VIII-XV. Carnegie Inst. Washington.
- Wilson, E. B., '09a. Recent Researches on the Determination and Heredity of Sex. *Sci.*, Vol. 29, No. 732, January 8, 1909, pp. 53-70.
- , '09b. Secondary Chromosome Couplings and the Sexual Relations in *Abraxas*. *Sci.*, Vol. 29, No. 748, April 30, 1909, pp. 704-706.
- Wood, T. B. Note on the Inheritance of Horns and Face-colour in Sheep. *Jour. Agri. Sci.*, Vol. I, Pt. 3, p. 364.